EVOLUTION OF THE SCALE-EATING CICHLID FISHES OF LAKE TANGANYIKA: A GENERIC REVISION WITH A DESCRIPTION OF A NEW SPECIES

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CONTENTS

ABSTRACT. A new scale-eating cichlid, *Perissodus eccentricus*, from Lake Tanganyika has been discovered, differing from all other lepidophagous Tanganyikan cichlids in its asymmetrically suspended jaws, low dorsal spine count and asymmetrically arranged jaw teeth. All lepidophagous cichlid species of Lake Tanganyika share a unique combination of one dental, one neurocranial, three mandibular, one maxillary, one palatal, and one branchial specializations. Because of a basic homogeneity in its specialized and unique morphology, the lepidophagous assemblage is considered monophyletic with all constituent species classified into one single genus, *Perissodus*. On phylogenetic grounds, it is proposed that *Plecodus* and *Xenochromis* be regarded as invalid genera. All specializations are adaptive integrations of structural elements to provide: a powerful and stable jaw closing mechanism; a capacity to open the mouth widely; highly mobile upper pharyngeal jaws which, in close coordination with the lower pharyngeal jaw, can arrange scales into manageable packets prior to deglutition. Interspecific relationships have been established on the basis of shared specializations in dentition, osteology and myology. Within the lineage we can detect an evolutionary trend towards occupation of progressively narrower adaptive zones. The simple morphogenetic mechanisms underlying this pronounced asymmetry are bilateral differences in differential growth rates of two bones in the jaw suspension and the remodeling of articular surfaces of the lower jaw joints. It is suggested that the anatomy of the new species, with its asymmetrical jaw suspension, furnishes further evidence that the underlying evolutionary mechanism involved in the explosive radiation of lacustrine cichlids is differential growth in various skull-elements.

INTRODUCTION

Lepidophagous cichlid fishes endemic to Lake Tanganyika are thought to be of diphyletic origin (Regan, 1920; Poll, 1950, 1956). Within the diphyletic pattern, *Perissodus microlepis* Boulenger 1898, represents a specialized monotypic genus with a pharyngeal apophysis composed of the parasphenoid only. Such a simple composition of the pharyngeal apophysis has been regarded as an indicator of phyletic origin from a *Tilapia*-like ancestor. In contrast, all species of the genus *Pleco-*

dus (*sensu* Boulenger, 1898) and *Xenochromis* (*sensu* Boulenger, 1899) possess a pharyngeal apophysis to which both the parasphenoid and basioccipital contribute, allegedly reflecting phyletic affinity with the genus *Haplochromis*. Wickler (1963) and Fryer and Iles (1972) have challenged the validity of using these two character states of the pharyngeal apophysis in establishing phyletic relationships within the family Cichlidae. In some species we have observed that the inclusion of the basioccipital in the apophysis is variable to such an extent that left and right sides of an individual specimen may differ. So far we have failed to determine which of the two character states represents the derived condition. This makes it virtually impossible to use the anatomy of the apophysis meaningfully in our phyletic analysis. Because of the paucity of evolutionary data on the various characters, the phyletic pattern of lepidophagous cichlids of Lake Tanganyika as conceived by Regan (1920) remains open to alternative interpretations.

The discovery of a new species of scaleeating cichlid with either sinistral or dextral asymmetry of the jaw teeth and representing a deep-water counterpart of *P. microlepis* has shed new light on the evolutionary mechanism underlying the adaptations to scale-eating. Jaw dentition of the juvenile of the new form is asymmetrical as in adults, but the anterior mandibular teeth are of the specialized form characterizing *Perissodus* (*sensu* Boulenger) whereas the form of the lateral premaxillary teeth is typical for *Plecodus* (*sensu* Boulenger). Subsequent analysis of jaw dentition of all scale-eating cichlids of Lake Tanganyika has revealed that the jaw teeth of *P. microlepis* are not unique, but are, in fact, characteristic of the group as a whole, encompassing all known species of *Perissodus, Plecodus* and *Xenochromis*.

In this study, we will attempt the following: (1) to offer an anatomical profile of the new species since it exhibits key phylogenetic characters for all lepidophagous cichlids of Lake Tanganyika; (2) to analyze comparative and functional aspects of the osteology and myology of all species within the lepidophagous group; (3) to determine the interrelationships within this trophic group and to offer a generic revision; and (4) to discuss the possible evolutionary pathway leading to the unique asymmetry in the new species.

MATERIALS AND METHODS

Proportional measurements and meristic counts are essentially those used by Thys van den Audenaerde (1964). The extent to which the last soft dorsal and anal finray elements were separated from their preceding element was variable; counts presented (see Table 2) are for all elements irrespective of whether or not the last two are joined at the base. Measurements are taken to the nearest 0.1 mm.

The specimens listed below have been examined from the following institutions: British Museum of Natural History (BMNH), Museum of Comparative Zoology (MCZ), Tervuren Museum, Belgium (TM), University of Michigan Museum of Zoology (UMMZ), and United States National Museum (USNM):

Perissodus eccentricus sp. n.: UMMZ 196003, 196004, 196056, 196005, 196006; MCZ 50092, 50093; TM 74–27–P–1; BMNH 1975.1.28:1.

Perissodus microlepis Boulenger: BMNH 1898 9.9.61 (holotype), 1960 9.30.6388– 6391; MCZ 49332; UMMZ 196000, 196002, 196001.

Perissodus burgeoni David: TM 38892– 38896 (types).

Perissodus gracilis Myers: USNM 102111 (paratypes).

Plecodus paradoxus Boulenger: BM 1960 9.30.6468–6482; MCZ 49330.

Plecodus straeleni Poll: MCZ 49328.

Plecodus multidentatus Poll: BM 1960 9.30.60528–60529 (paratypes); MCZ 49543, 49544, 49545.

Plecodus elaviae Poll: MCZ 49331.

Xenochromis hecqui Boulenger: BM 692,

Table 1.   Morphometric characteristics in per mille standard length or per mille head length (*) of *P. microlepis* and the type series of *P. eccentricus*.

| Character | *eccentricus* | | *microlepis* | | |
	Holotype	Holotype and 14 paratypes	Holotype	*P. gracilis*, 2 paratypes	7 specimens from Zambia
Total length, mm	164	81–164	95		
Standard length, mm	128	64–128	81	46– 54	55–103
Body depth	289	257–289	247	243–249	255–287
Head length	305	293–334	288	306–356	289–310
Caudal peduncle length,	198	163–202	177	178–180	161–172
least depth	105	104–115	121	102–108	106–117
Last dorsal spine length	130	124–145	109	114	110–126
Third anal spine length	138	136–166	105	106–117	110–129
Pectoral length	284	264–293			
Pelvic length	250	244–285			
Orbit diameter*	349	315–373	290	299–315	256–304
Interorbital bony width*	256	240–267	298	213–248	247–315
Snout length*	295	278–307	274	335–382	298–356
Preorbital depth*	82	66– 90	95	55– 60	63– 91
Premaxillary pedicle length*	210	191–210	179	171–182	157–203
Mandible length*	385	299–385	369	317–339	305–343

1960 9.30.6364–6369, 1960 9.30.6381–6386, 1950 4.1.5097–5103, 1960 9.30.6370–6373, 1960 9.30.6376–6380; MCZ 49333, 49334.

With a few exceptions, osteological and myological nomenclature follows that of Liem (1970), and Winterbottom (1974), respectively.

Scanning electron micrographs are based on excised jaws which have been cleaned with diluted solutions of sodium hypochlorite, dehydrated in absolute alcohol, mounted with silverpaint and coated with gold.

Perissodus eccentricus new species
Figure 1, Tables 1 and 2

Holotypes: UMMZ 196003, 128 mm (164 mm TL); Paratypes· UMMZ 196004, 3:102–121 mm; UMMZ 196056, 5:109–117 mm; UMMZ 196005, 2:92–94 mm; UMMZ 196006, 2:86–88mm; BMNH, 1975.1.28:1:1:91 mm; MCZ 50093, 1:121 mm; MCZ 50092, 1:92 mm (alizarin prep.); MCZ 50718, 1·63.5 mm (formerly TM 112610); TM 74–27–P–1, 1:122 mm.

Description. Differs from other lepidophagous Tanganyikan cichlids by its asymmetrical jaw teeth and low dorsal spine count (14–15 cf. 16–20). Jaws suspended asymmetrically in such a way

that a given individual can only use one side of its mouth to bite scales from prey. Dextral-jawed specimens have left side of most teeth of both the upper and lower jaws abraded at an angle and variously slanting laterally to the right; right side of mandible is lower and jaws project to the right when opened (Plates 1, 2, Figs. 17–22). Sinistral- and dextral-jawed specimens are equally abundant. Two specimens had a row of 11–16 pored scales above the upper lateral line and contiguous with the base of the soft dorsal fin. Such an elaboration of the lateral line has not been reported for any cichlid to our knowledge.

P. eccentricus is closely allied to *P. microlepis* from which it differs further as follows: (1) has more upper and lower lateral line pores, upper lateral line extends posteriorly beyond end of dorsal fin base (cf. not beyond end) and lower lateral line extends forward to tip of pectoral fin (cf. not reaching pectoral fin); (2) has longer last dorsal and anal spines; (3) has larger orbits; when comparing similar sized specimens, orbit (as a percentage of head length) provides a 100% dichotomy but because of negative allometry of orbit
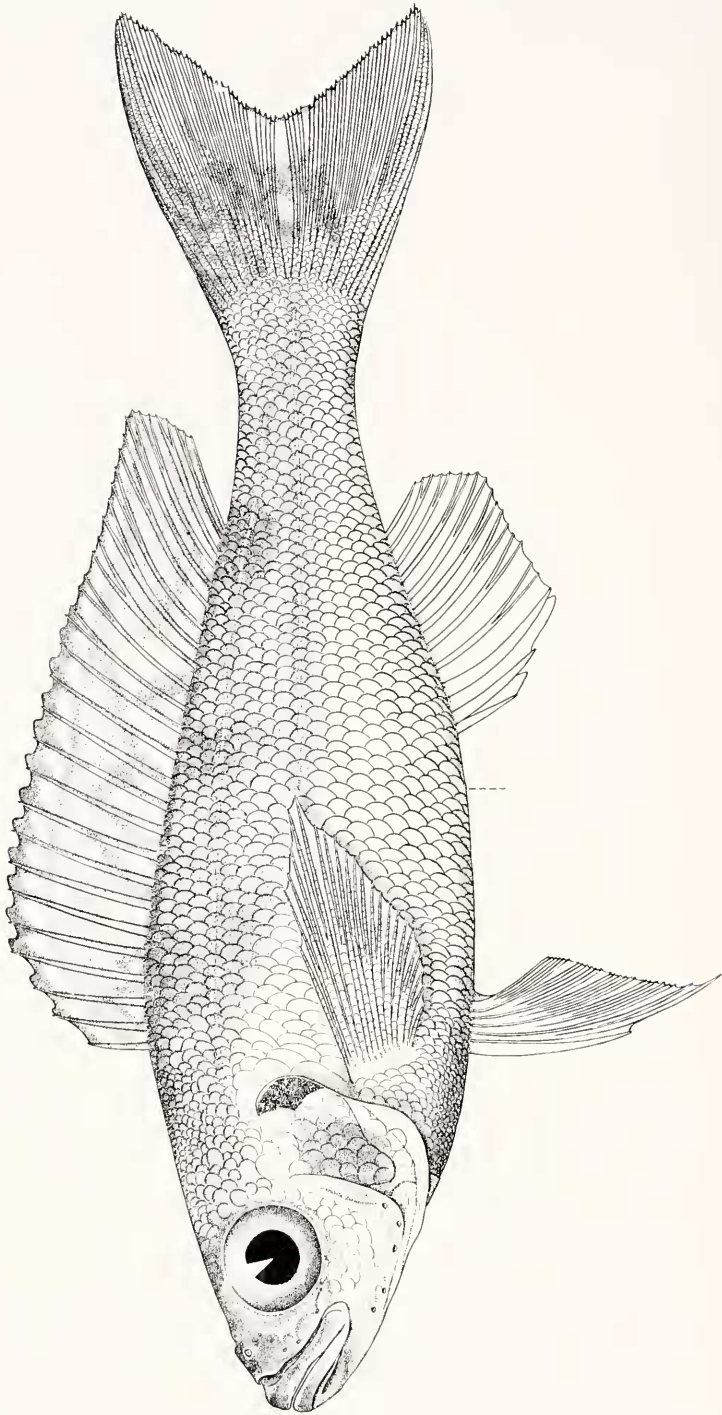
TABLE 2.   MERISTIC CHARACTERISTICS OF *P. MICROLEPIS* AND THE TYPE SERIES OF *P. ECCENTRICUS*.

Character	eccentricus		microlepis		
	Holotype	Holotype and 14 paratypes	Holotype*	P. gracilis, 2 paratypes	7 specimens from Zambia
Dorsal fin spines,	XIV	XIV–XV	XVIII	XVII	XVII–XVIII
rays	11	10–13	11(10)	11–12	10–11
Anal fin	III, 9	III, 9–11	III, 9(8)	III, 9–10	III, 9–11
Upper lateral line scales	57	51–60	47(44)	45–46	44–51
Lower lateral line scales	37	32–45	31	21–25	25–31
Lateral line scales	64	63–69	65	67	62–70
Transverse scale rows	5.5/18	5.5–7/16–18	(5/20)		
Cheek scale rows	3	2–3	(3)	3	3
Circumpeduncular scales	27	27–31	30	28–29	29–30
Premaxillary teeth	23	20–24	23(20)	19–22	20–27
Mandibular teeth	17	14–18	19(18)	16	16–21
Gillrakers	17+1+5	(16–19)+1+(4–6)	18+1+7(14)	(19–20)+1+7	(18–20)+1+(6–7)
Vertebrae	15+18				

* Numbers in brackets are from original description by Boulenger (1898).

juvenile *P. microlepis* (< 50 mm) may have orbits as large as adult *P. eccentricus* (> 110 mm); (4) has terminal mouth (cf. superior mouth and projecting mandible); (5) has weakly developed melanophores on head and body; in preserved specimens, pelvic and anal fins clear, dorsal and caudal fin with faint grey mottlings (Figure 1). This is in sharp contrast to *P. microlepis* which usually has pelvic and vertical fins, head and body heavily pigmented, dark olive-brown in alcohol. Relatively large eyes and perhaps also the extended lateral line pores of *P. eccentricus* are believed to be sensory compensations for life in a dim habitat.

No obvious sexual dimorphism or dichromatism in preserved specimens; life colors are unknown.

The type series for *P. burgeoni* David 1936 and paratypes of *P. gracilis* Myers 1936 (Tables 1 and 2) were re-examined to be sure *P. eccentricus* was not involved. With respect to diagnostic characters mentioned above, all specimens agreed with *P. microlepis;* we concur with Poll (1946, 1956) in synonymizing these taxa with *P. microlepis*.

Etymology. Eccentricus, from Greek *ekkentros,* from *ex* (out of) + *kentron* (center). This name seems appropriate as it alludes to asymmetry of the teeth and jaws as well as the strange or unconventional morphology and inferred feeding behavior.

Food habits. All stomachs of *P. eccentricus* which were not empty contained only fish scales most or all of which were from cichlids. As all specimens except the one juvenile were taken in deep-water gill nets, our analysis of food habits could be biased against rapidly digested items.

Distribution. Endemic to Lake Tanganyika; adults known only from 60–100 m depths in Zambia—Musende Bay, Chituta Bay and off Mwela; one juvenile collected in a trawl 5 km east of Kalemié (formerly Albertville), Republique du Zaire at 70–100 m. Depth distribution is complementary to that of *P. microlepis* which is abundant in water less than 15 m deep and has a maximum verified depth range to 40 m (Poll 1956).

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Figure 1.   *Perissodus eccentricus*, holotype, UMMZ 196003, male, Chituta Bay, 100 m, Lake Tanganyika, Zambia. Lateral view. (Drawn by Patricia Chaudhuri.)
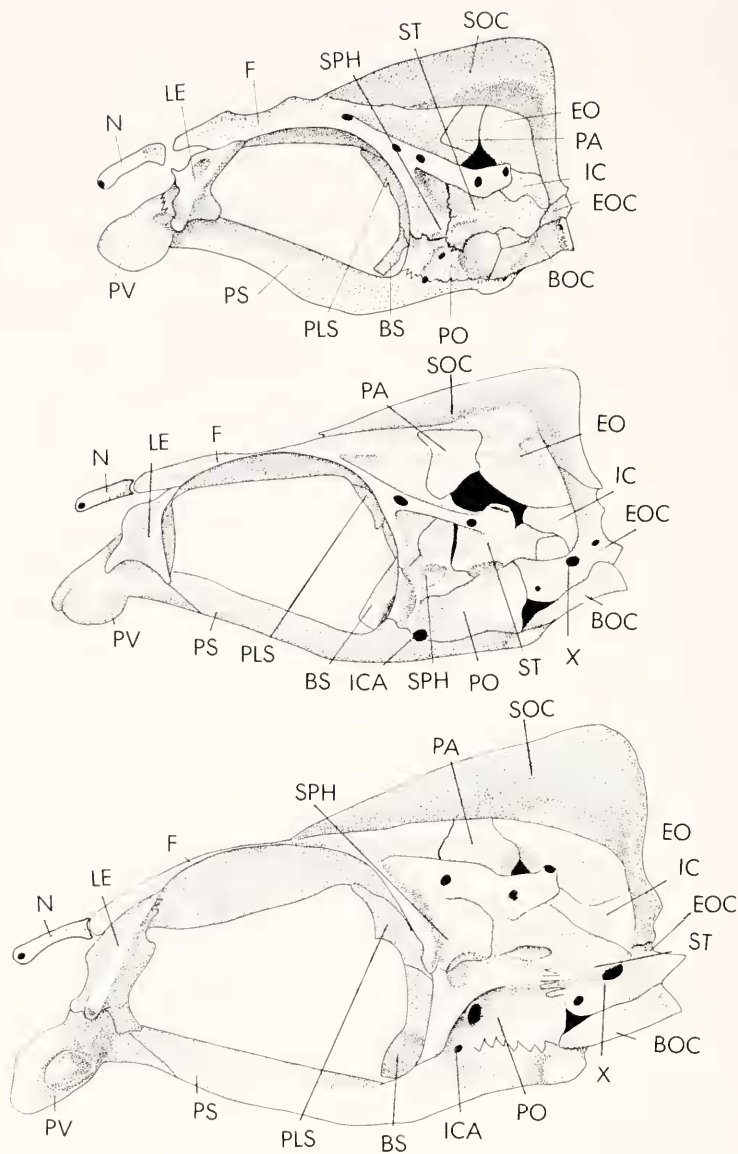
Figure 2.   Lateral aspect of neurocranium. A, *eccentricus*; B, *microlepis*; C, *hecqui*.

SOME OSTEOLOGICAL ASPECTS OF *P. ECCENTRICUS*

Neurocranium

The marked asymmetry of the suspensory apparatus has not affected the bilateral symmetry of the neurocranium.

The roof of the neurocranium (Fig. 4A)

conforms to that of more generalized cichlids as described by Greenwood (1967, 1974), Vandewalle (1972) and Goedel (1974a, b). However, several distinguishing features can be recognized in *P. eccentricus*. Anteromedially the cranial roof possesses a shallow and rather restricted rostral fossa the floor of which is

made up solely by the ethmoid (Fig. 4A: E, PV, F). In the ethmoid region, there is a sutural junction between ascending processes of the vomer with the lateral ethmoid. Very restricted connections are present between the ethmoid and ascending processes of the vomer (PV).

Although highly specialized in some features, the neurocranium of *P. eccentricus* retains such primitive characteristics as the

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KEY TO ABBREVIATIONS

|	
A:	articular
A_1:	adductor mandibulae pars A_1
A_2:	adductor mandibulae pars A_2
AAP:	adductor arcus palatini
AD:	adductor branchialis
ADA:	ascending process of articular
AM_1:	adductor mandibulae pars A_1
AM_2:	adductor mandibulae pars A_2
AM_3:	adductor mandibulae pars A_3
AO:	adductor operculi
AP:	articular process
APA:	ascending process of articular
APD:	ascending process of dentary (coronoid)
APPM:	ascending process of premaxilla
BL:	Baudelot's ligament
BOC:	basioccipital
BS:	basisphenoid
BSR:	branchiostegal ray
CB:	ceratobranchial
CB_5:	fifth ceratobranchial (lower pharyngeal jaw)
CC:	cranial condyle
CL:	cleithrum
D:	dentary
DO:	dilatator operculi
E:	ethmoid
EB:	epibranchial
ECT:	ectopterygoid
ENT:	entopterygoid
EO:	epiotic
EOC:	exoccipital
EP:	epaxial muscles
ES:	esophagus
F:	frontal
GHA:	geniohyoideus anterior
GHP:	geniohyoideus posterior
HH:	hyohyoideus
HHI:	hyohyoideus inferior
HHS:	hyohyoideus superior
HM:	hyomandibula
HY:	hyoid
IAM_{1-2}:	intramandibularis 1 and 2
IC:	intercalary
ICA:	foramen for internal carotid artery
IML:	interoperculomandibular ligament
IOP:	interoperculum
L:	ligament
LAP:	levator arcus palatini
LE:	lateral ethmoid-prefrontal complex
LE_4:	fourth levator externus
LEM:	levator externus muscle
LI:	levator internus
LIM:	interoperculomandibular ligament
LO:	levator operculi
LP:	levator posterior
M:	mandible
MD:	mandible
MMM:	collagen tract within lower lip
MPT:	metapterygoid
MX:	maxilla
N:	nasal
OD:	obliquus dorsalis
OF:	obliquus posterior
OP:	operculum
P:	palatine
PA:	parietal
PB_1:	first pharyngobranchial
PC:	premaxillary condyle
PCE:	pharyngocleithralis externus
PCI:	pharyngocleithralis internus
PF:	prefrontal-lateral ethmoid complex
PHH:	rectus communis (pharyngohyoideus)
PLS:	pleurosphenoid (pterosphenoid, alisphenoid)
PM:	premaxilla
PO:	prootic
POP:	preoperculum
PP:	postmaxillary process of maxilla
PPM:	protractor pectoralis
PS:	parasphenoid
PV:	vomer
Q:	quadrate
RP:	retractor dorsalis (retractor ossium pharyngealium)
SCL:	supracleithrum
SH:	sternohyoideus
SOC:	supraoccipital
SOP:	suboperculum
SPH:	sphenotic
ST:	pterotic (supratemporal)
SY:	symplectic
TAM:	tendon of adductor mandibulae
TDA:	transversus dorsalis anterior
TDA_{1-3}:	transversus dorsalis anterior parts 1–3
TDP:	transversus dorsalis posterior
UH:	urohyal
V:	vertebra
X:	foramen of vagus nerve
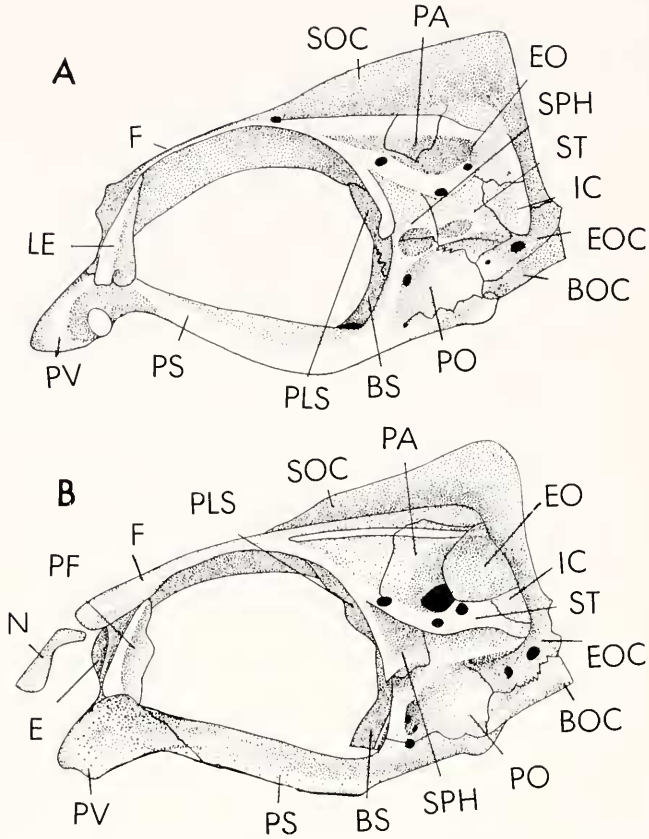
Figure 3.   Lateral aspect of neurocranium. A, *multidentatus*; B, *paradoxus*.

somewhat decurved dorsal profile to the preorbital face, the high cranial vault and the relatively short ethmovomerine region (Fig. 2A). At the orbital level, the parasphenoid turns dorsally to join the ethmovomerine complex giving the cranial base a pronounced curved profile. Posteriorly the long axis of the basioccipital makes a 25 degree angle with the horizontal plane. The relatively small pharyngeal apophysis is formed from the parasphenoid only.

Suspensory Apparatus

Bilateral asymmetry is especially pronounced in the anterior part of the suspensory unit, the posterior half being symmetrical.

In dextral individuals the right palatine-maxillary joint is located more posteriorly and laterally than the left joint (Fig. 15A). The depth of the suspensory apparatus measured from the dorsal rim of the body of the palatine to the ventral edge of the condyle of the quadrate is much greater on the left side (Fig. 15C) in dextral individuals. Consequently, the quadrato-mandibular joint in dextral individuals is positioned more dorsally on the right side (Fig. 15B, C).

The suspensory apparatus in dextral individuals is distinctly longer on the left side when measured between the anterior tip of the maxillary process of the palatine and the anterior edge of the anterior head of the hyomandibular. Yet the left and right palatines and hyomandibulars exhibit

identical proportions and shapes. Asymmetry appears to have arisen by differences in orientation and proportions of the quadrate-symplectic complex. Dextral individuals possess a more horizontal and relatively shorter symplectic and an anteriorly rotated quadrate on the right side. Unlike the right one, the left quadrate has a vertically orientated cranial border (Fig. 16).

Exceptionally strong sutural connections between the symplectic process of the hyomandibular, metapterygoid, entopterygoid, and palatine bones may add strength to the suspensory apparatus, which must be able to absorb considerable forces during the "bite." Additional adaptations to withstand exceptionally strong forces have evolved in the head of the palatine which is firmly anchored to the vomer and prefrontal by unusually well-developed processes. The metapterygoid and entopterygoid are enlarged, forming mediodorsally directed shelflike extensions partially bridging the gap between the parasphenoid and the suspensory apparatus. A well-developed adductor fossa in the preoperculum accommodates the A_2 and A_3 parts of the adductor mandibulae muscle (Fig. 5A POP).

Jaw Apparatus

Asymmetry is especially evident during opening and protrusion of the jaws. Both upper and lower jaws deviate either to the left or right side respectively in sinistral and dextral individuals. However, no asymmetrical features have been found between left and right sides of the premaxillae, maxillae and dentaries. Noticeably asymmetrical differences in the mandible are confined to the left and right articulars.

In the mandible, the extraordinarily well-differentiated dentary has become by far the most dominant component, occupying almost the entire length of the dorsal mar-
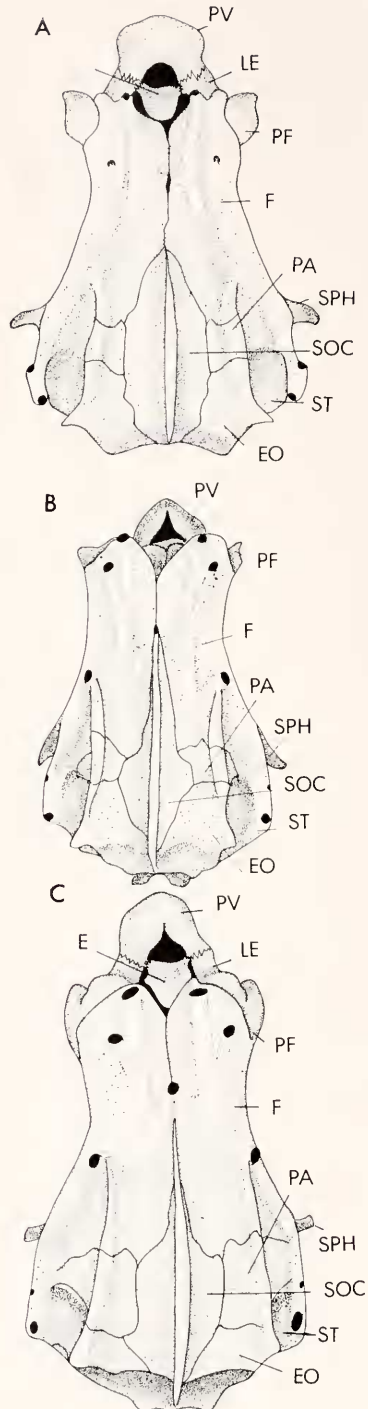
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Figure 4. Dorsal aspect of neurocranium. A, *eccentricus*; B, *paradoxus*; C, *microlepis*.
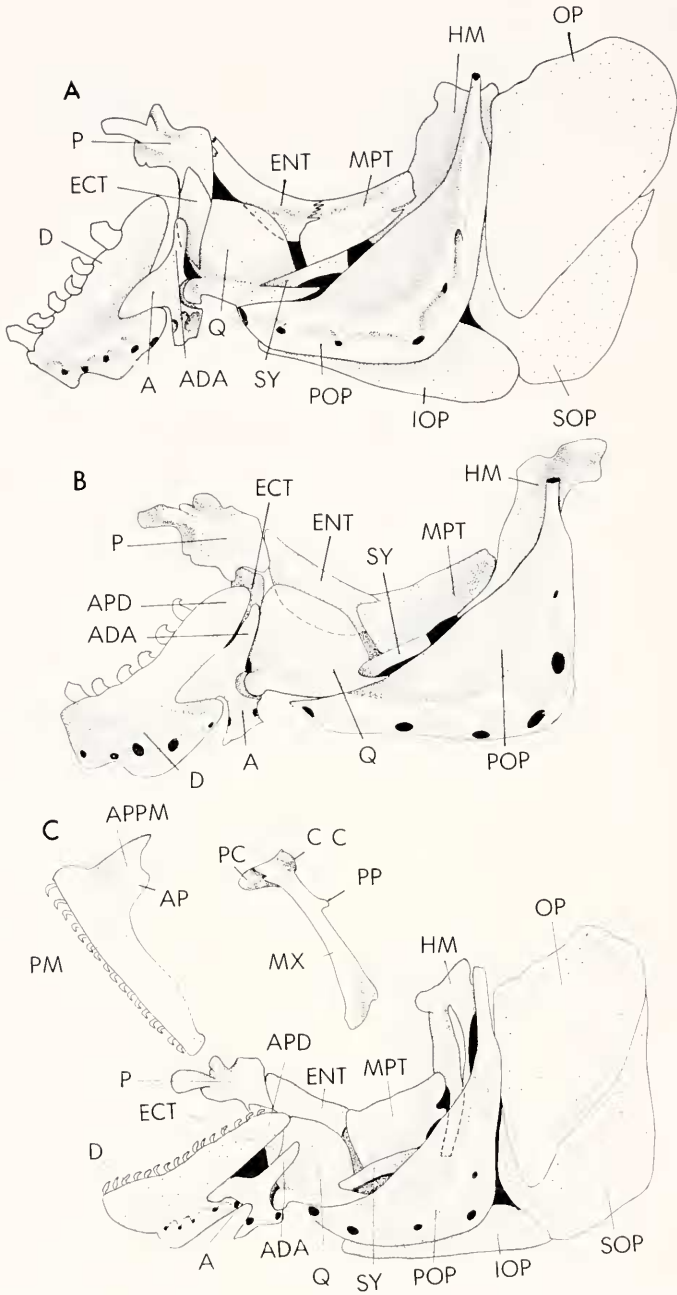
Figure 5. Lateral aspect of suspensory apparatus and mandible. A, *eccentricus*, opercular apparatus included; B, *microlepis*; C, *multidentatus*, opercular apparatus and upper jaw included.
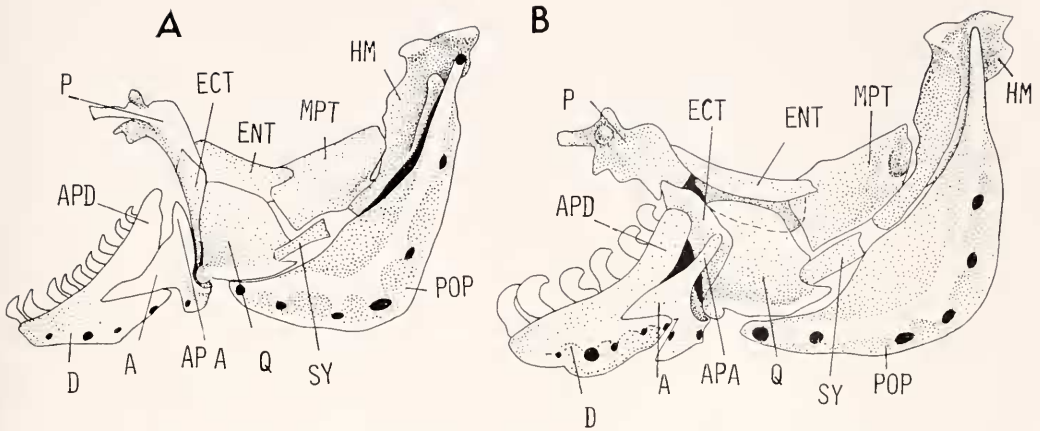
Figure 6.   Lateral aspect of suspensory apparatus and mandible. A, *hecqui*; B, *paradoxus*.

gin and forming about 70 percent of the total mandibular length ventrally. A deep notch in the ventral margin of the dentary at the level of the second mandibular pore gives the mandible a characteristic lateral profile (Fig. 5A:D). The most outstanding mandibular feature is the topography of the ascending process of the dentary, which reaches dorsally to the middle of the maxilla when the jaws are fully opened. Compared with the dentary, the articular is small, although it possesses a high slender ascending process. In dextral individuals, the articulatory surface of the right articular socket is deeper and more nearly U-shaped in lateral view compared with the left articular (Fig. 16). The articulatory head of the right quadrate is smaller and directed more anteriorly in dextral individuals, while that of the left quadrate is larger and directed more ventrally.

The premaxilla has a very long alveolar process while the ascending process is exceptionally short and slender. Flanking the ascending process is a prominent articular process (Fig. 7A:AP, APPM).

The maxilla is distinctly elongate and rather slender with a concave anterior margin. Ventrally the body of the maxilla ends in a slender process. Originating from the posterior margin slightly above the middle of the maxillary body is a character-

istically well-developed process hence called the postmaxillary process (Fig. 7A: PP). The premaxillary condyle is long and stout and originates from the body of the maxilla at an angle of about 30 degrees. The proximal tip of the maxillary body is blunt and abbreviated.

MYOLOGICAL ASPECTS OF *P. ECCENTRICUS*

Although the adductor-mandibulae complex conforms to that of other cichlids as described by Vandewalle (1972), Goedel (1974a, b), and Liem and Osse (1975), four important specializations (Fig. 8A) have evolved in *P. eccentricus*: (1) The adductor mandibulae pars A_2 is clearly subdivided into a dorsal head which inserts on the ascending (coronoid) process of the dentary by means of an aponeurosis passing medially to the ascending process of the articular (cf. Goedel, 1974a, who illustrates a lateral passage in Fig. 18b but describes a medial topography on p. 258). The ventral head, originating mainly from the horizontal limb of the preopercular and symplectic, inserts via an aponeurosis on the posterior aspect of the slender ascending process of the articular (Fig. 10A); (2) Pars A_3 of the adductor mandibulae complex is greatly reduced although it maintains the same topography as in

Tilapia; (3) A considerable shortening in relative length of the muscle fibers of the adductor arcus palatini has accompanied the approximation of the dorsal rim of the suspensory apparatus and the parasphenoid. Concomitant with fiber length shortening, both the anterior and posterior extents of the adductor arcus palatini have been reduced; (4) The intramandibular division of the adductor complex (m. mentalis of Goedel, 1974a, b; the quadrato-dentaire of Vandewalle, 1972) is distinctly differentiated into two independent entities (Fig. 10B). One dorsal subdivision represents the original intramandibularis muscle ($Aw = IAM_1$) retaining the typical topography. The larger, more ventral subdivision (IAM_2) includes a strong tendon beginning at the medial aspect of the quadrate at the quadratomandibular joint level and inserting on the entire medial surface of the mandible ventral to the dorsal part of the intramandibularis muscle. Goedel (1974a, b) does not mention such a subdivision in *Tilapia tholloni*, but Vandewalle has recorded the presence of a separate head ("muscle quadrato-dentaire") in *Tilapia guineensis.*

The hyoid and opercular musculature in *P. eccentricus* conform with generalized cichlids in the levator arcus palatini (LAP), dilatator operculi (DO), levator operculi (LO), adductor operculi, adductor hyomandibulae and adductor operculi muscles (Fig. 8A). However, the geniohyoideus anterior and posterior in *P. eccentricus* (Fig. 11) form a much more elongate compound muscle with two distinct tendinous inscriptions, indicating a capability to produce greater excursions of the hyoid apparatus and mandible. The hyohyoideus superior and inferior and the sternohyoideus (Fig. 11:HHS, HHI, SH) exhibit the same topography and morphology found in generalized cichlids. Such a retention of a basic integration of the hyoid and branchiostegal elements may be correlated with the exceptional efficiency of this functional complex in respiration. In *P.*

eccentricus the hyohyoideus inferior is greatly reduced.

Although the branchial and pharyngeal muscles in *P. eccentricus* do not deviate much from those found in the characteristic cichlid body plan as described by Liem (1973), and Liem and Osse (1975), some salient specializations have been found. The transversus dorsalis anterior is greatly reduced with the total loss of one head, while the second and third heads are rudimentary. The third head has lost its connections to the parasphenoid (Fig. 13A:TDA). Although still relatively well-differentiated, the transversus dorsalis posterior (Fig. 13A:TDP) has undergone marked reduction compared with the condition in generalized cichlids. Marked hypertrophy of the first levator internus (Fig. 13A:LI) gives the branchial musculature a unique appearance. The second levator internus has remained unmodified. The rectus communis (pharyngohyoideus) is very prominent ventrally both in length and cross section (Fig. 12A:PHH). A tendon divides the rectus communis into two distinct bellies. The pharyngocleithralis externus, a functional antagonist of the rectus communis, has also undergone significant hypertrophy (Fig. 12A:PCI). As in all cichlids, the fourth levator externus is composed of a rudimentary lateral head inserting on the dorsal aspect of the fourth epibranchial by means of an aponeurosis, whereas the dominant medial head (identified by Goedel, 1974 [a, b] as a protractor arcuum branchialium, a *de novo* muscle development) inserts on the muscular process of the lower pharyngeal jaw.

COMPARATIVE ANATOMY OF THE SCALE-EATING GROUP

Having outlined the main morphological features of this highly specialized new species, we can consider the anatomy of all other lepidophagous cichlids of Lake Tanganyika, grouped into three separate genera by previous authors:
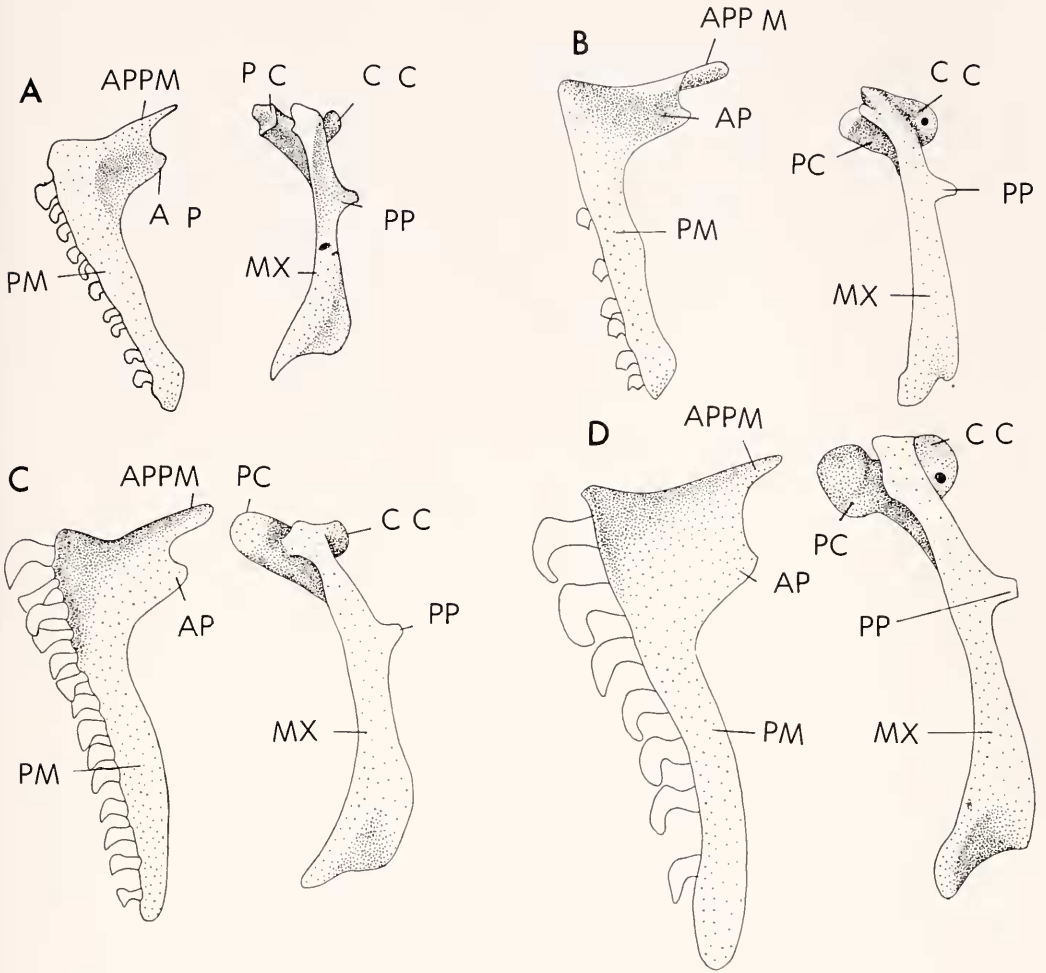
Xenochromis Boulenger 1899 has been

Figure 7.   Lateral aspect of upper jaws. A, *eccentricus*; B, *microlepis*; C, *hecqui*; D, *paradoxus*.

maintained in a monotypic genus because of presumed planktivorous feeding habits (Poll, 1956, p. 413) and its dentition composed of obtusely pointed and posteriorly recurved small teeth arranged in a single row numbering 22–45 on the upper jaw and 19–40 on the lower jaw. However, our studies on stomach contents have revealed that X. *hecqui* feeds predominantly on scales of cichlids. We are therefore including X. *hecqui* into the lepidophagous trophic category.

Perissodus Boulenger 1898 represents a monotypic genus; it is characterized by broad-based truncated teeth arranged in a single row numbering 18–26 and 16–18 respectively on the upper and lower jaws.

Plecodus Boulenger 1898 with four species (*paradoxus, elaviae, straeleni,* and *multidentatus*) has laminar, strongly recurved or curled teeth. In the type species, *paradoxus*, the teeth are arranged in a single row numbering 18–20 and 12–15 respectively on the upper and lower jaws.

Neurocranium

The skull roof is broad both interorbitally and across the otic region in all lepidophagous species. Characteristic features of this lepidophagous skull type are the relatively decurved dorsal profile giving the orbital margin a rounded circumference, a rather high cranial vault and the relatively short ethmovomerine region. All these neurocranial features correspond with those of the generalized *Haplochromis bloyeti* as described by Greenwood (1974) and *H. burtoni*. However, all lepidophagous neurocrania deviate from the generalized form in three specializations: (1) The parasphenoid, at the level of the posterior orbit, slopes forwards and upwards when viewed laterally (Figs. 2, 3:PS). Such an abrupt angling of the parasphenoid gives the lepidophagous neurocranium a very unique lateral profile, not generally encountered in other trophic groups; (2) The preorbital region is shorter, with a more vertically oriented prefrontal-lateral ethmoid complex; (3) well-differentiated apophyses, representing attachment sites for the palatine, are present on the lateral aspect of the ethmoid (Figs. 2, 3:PF, LE, E) and the lateral flange of the lateral ethmoid-prefrontal.

Interspecific differences are mostly confined to the preorbital region. The floor of the rostral fossa in the cranial roof is formed by anteromedial shelves of the frontals in *paradoxus, straeleni, elaviae,* and *multidentatus* (Fig. 4B), whereas in *hecqui, microlepis* and *eccentricus* the ethmoid is also involved in the composition of the floor of the rostral fossa (Fig. 4:A, C, E). Concomitantly the lateral ethmoid-prefrontal complex is more vertical in *paradoxus, elaviae, straeleni* and *multidentatus* (Figs. 2, 3:PF, LE) than in *hecqui, microlepis* and *eccentricus*. The supraoccipital crest is relatively low and does not extend farther anteriorly than midway between the orbits (Figs. 2, 3:SOC), except in *straeleni* in which the high occipital crest reaches the posterior rim of the rostral fossa.

Suspensory Apparatus

All lepidophagous species share the following specializations in the suspensory apparatus (Figs. 5, 6): (1) strong, sutural connections between the following pairs of bones, the symplectic process of the hyomandibular-metapterygoid, the metapterygoid-entopterygoid, and the palatine-ectopterygoid; (2) the vertical and horizontal limbs of the preoperculum are at a 90 degree or nearly 90 degree angle to each other and enclose a prominent adductor fossa; (3) the large palatine has large vomerine and prefrontal processes.

Only a few interspecific differences have been found in the suspensory apparatus. The palatine in *hecqui* (Fig. 6A:P) is more slender than in other species, although it has well-differentiated prefrontal and vomerine processes. Vertically oriented ectopterygoids are found in *microlepis, eccentricus* and *straeleni* whereas in *paradoxus, multidentatus* and *hecqui* the bones are slightly oblique (Figs. 5, 6:ECT).

Jaw Apparatus

A unique specialization of the maxilla shared by all lepidophagous cichlids of Lake Tanganyika is a prominent process originating from the posterior margin of the maxilla (Figs. 5, 7:MX, PP). This blunt but slender posterior maxillary process is directed caudally. Neither muscle nor special ligamentous attachments are associated with this process which is located within the connective tissue which extends between the upper jaw and the cheek. The function of the posterior maxillary process is unknown.

All lepidophagous species also share the following specializations: (1) The proximal tip of the maxillary body is blunt and abbreviated (Figs. 5, 6, 7:MX); (2) Ventrally the maxilla possesses an extra flange for attaching the enlarged maxillomandibular ligament; (3) The premaxillae have short ascending processes and prominent articular processes (Figs. 5C, 7:APPM, AP); (4) The dentary is the dominant element in
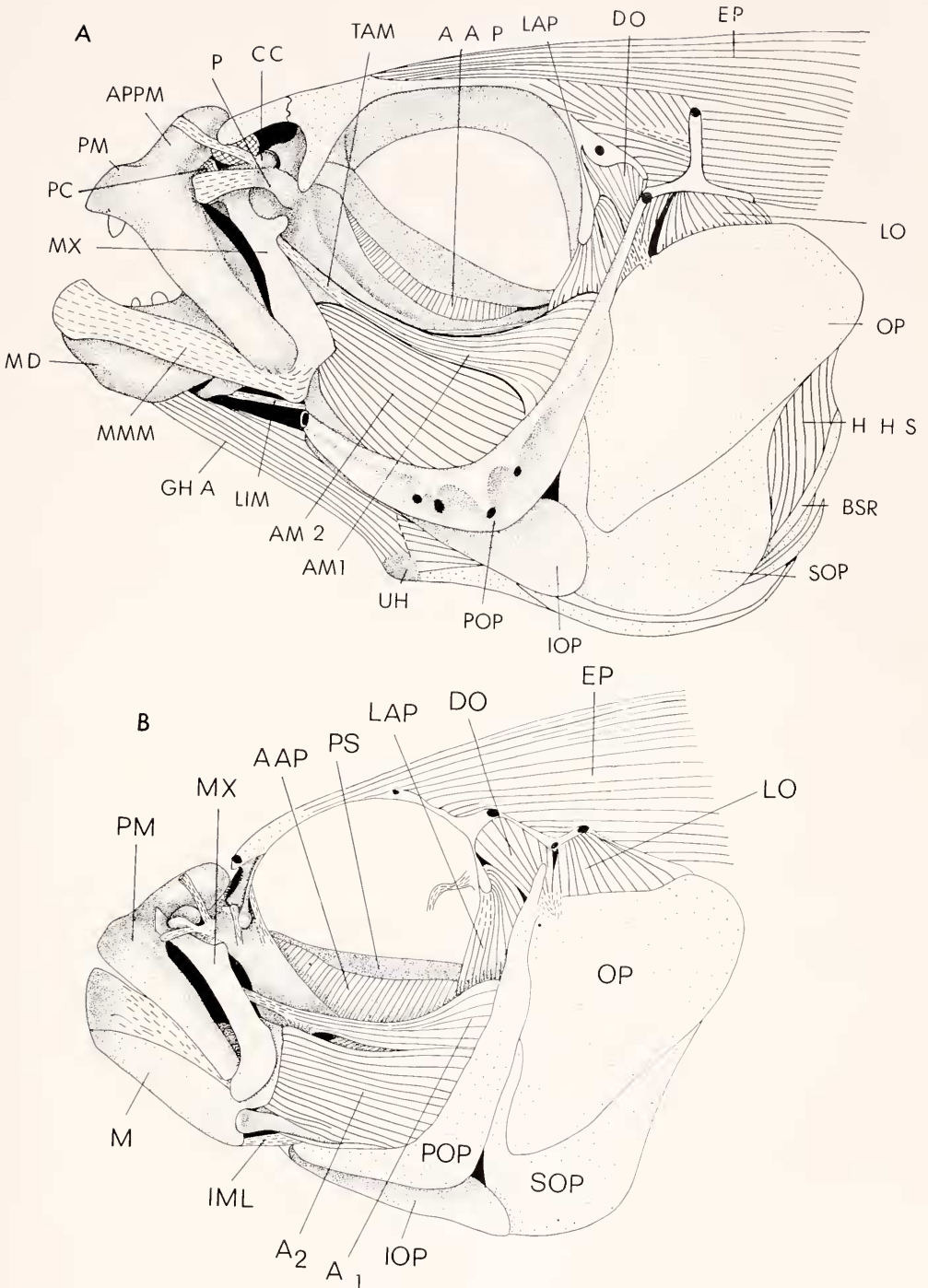
Figure 8. Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball. A, *eccentricus*; B, *hecqui*.
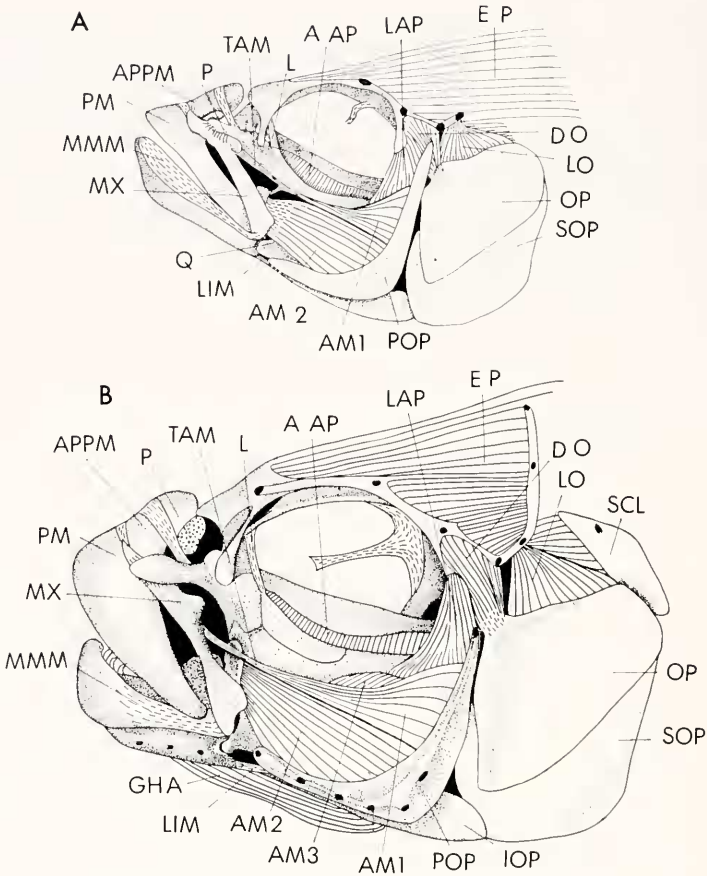
Figure 9. Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball. A, *microlepis*; B, *paradoxus*.

the mandible; the small anguloarticular is excluded from the dorsal margin, although it possesses a high ascending process (Figs. 5, 6:A, D).

Interspecific differences of the maxilla are especially discernable in the shape of the maxillary body. A strongly concave profile of the anterior margin of the maxilla is found in *hecqui*, *paradoxus*, and *eccentricus*, whereas in *microlepis* and *multidentatus* it is only slightly concave. Relatively long mandibles characterize *hecqui* and *multidentatus*, while *eccentricus*, *microlepis* and *paradoxus* possess shorter and deeper mandibles (Figs. 5, 6, 7:MX).

Intrinsic Ligaments of the Jaw Apparatus

All lepidophagous cichlids of Lake Tanganyika possess a very thick and broad ligament within the lower lip, extending from the anterior tip of the dentary to the ventral tips of the premaxilla and maxilla (Figs. 8, 9:MMM). Histologically, it appears as a prominent tract of collaginous fibers. This ligament may help stabilize the jaws especially when the mouth is opened widely during the bite. Concomitantly the maxillomandibulare mediale and anterius ligaments are hypertrophied. No inter-specific differences have been found.

Adductor Mandibulae Muscles

The intramandibular division of the adductor complex is divided into two distinct units in all lepidophagous cichlids of Lake Tanganyika (Fig. 10B:IAM$_1$:IAM$_2$). The dorsal head represents the original intramandibularis (adductor mandibulae pars A$_w$) retaining the typical topography, while the larger ventral head originates tendinously from the medial aspect of the quadrate at the quadratomandibular joint level and inserts on the medial surface of the mandible (Fig. 10B:IAM$_2$). Such a distinct subdivision also occurs in algae-scraping cichlids from Lake Tanganyika and Malawi, suggesting a role in closing the strongly abducted lower jaw.

Adductor Arcus Palatini

With the exception of *hecqui*, the lepidophagous cichlids are characterized by a reduction in relative fiber length of the adductor arcus palatini (Figs. 8, 9:AAP) and by the shelflike dorsal extension of the entopterygoid and metapterygoid. This extension narrows the distance between the parasphenoid and the dorsal rim of the suspensory apparatus. In *hecqui* (Fig. 8B: AAP), the adductor arcus palatini resembles that of more generalized cichlids (Goedel, 1974a, b; Liem and Osse, 1975).

Dorsal Branchial Muscles

All lepidophagous cichlids of Lake Tanganyika have a hypertrophied anterior levator internus (Fig. 13:LI) functioning as the antagonist of the retractor dorsalis (RP).

Other specializations shared by *microlepis, eccentricus, paradoxus, straeleni* and *elaviae* include: (1) Drastic reduction of all transversus dorsalis muscles. The transversus dorsalis anterior, originally composed of three separate heads, loses the second head which runs from the anterior surface of the second pharyngobranchial to partially blend into the longitudinal musculature of the esophagus while the
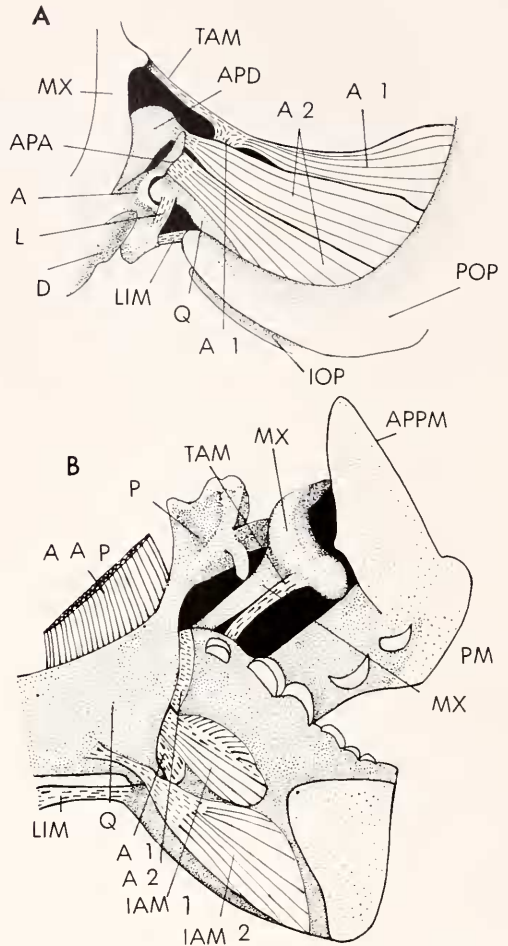

Figure 10. A, lateral view of adductor mandibulae muscles and surrounding bones in *eccentricus*; B, medial aspect of upper and lower jaws and associated muscles in *paradoxus*.

other fibers insert on the medial surface of the third and fourth pharyngobranchials. The third head (transversus obliquus) runs from the anterior surface of the second epibranchial to an aponeurosis from its fellow of the other side although there is always a small part with an aponeurotic attachment to the parasphenoid. Anteriorly the first head, which runs between the anterior surfaces of the pharyngobranchials, is retained in all lepidophagous cichlids, although it is greatly reduced in *eccentri-*
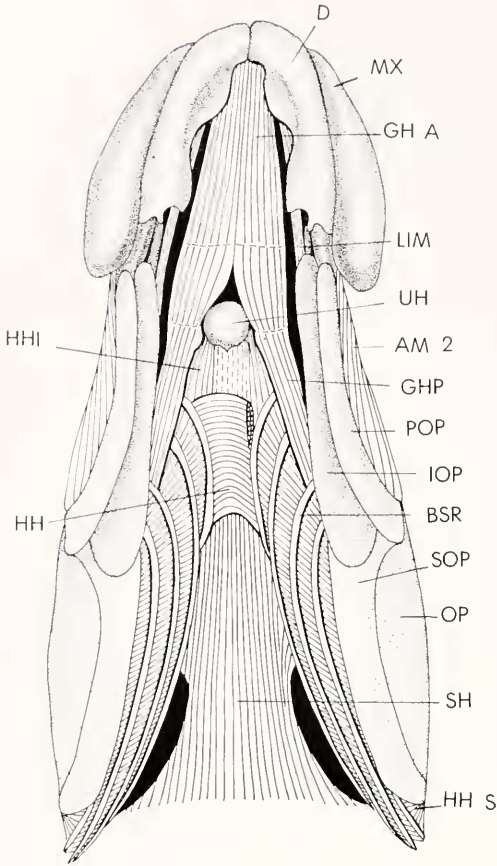
Figure 11.   Ventral aspect of muscles of the head of *eccentricus.*

cus (Fig.13:TDA, TDP); (2) The weakly developed transversus dorsalis posterior runs without interruptions between the tubercles on the dorsal aspects of the toothplates of the fourth branchial arch; (3) Another marked reduction affects the obliquus posterior which runs between the muscular process of the lower pharyngeal jaw (= fifth ceratobranchials) and the posteromedial face of the fourth epibranchial (Fig. 13:OF).

In *hecqui* and *multidentatus* the dorsal branchial musculature resembles that of the usual cichlid type, e.g., *Tilapia* (Goedel, 1974a, b). The three heads of the transversus dorsalis anterior (Fig. 13B, D:TDA)

are clearly differentiated and the obliquus posterior is not atrophied.

Ventral Branchial Musculature

Two muscles in this region play a dominant role in all lepidophagous cichlids of Lake Tanganyika. The rectus communis (pharyngohyoideus) is hypertrophied and possesses two bellies separated by either a tendon or tendinous inscription. Concomitantly its functional antagonist, the pharyngocleithralis internus, (Liem, 1973), (pharyngoclavicularis internus) is also hypertrophied (Fig. 12A, B:PHII, PCI).

DISCUSSION

Generic Revision

The generic identities of *Perissodus,* *Plecodus* and *Xenochromis* as originally envisioned by Boulenger (1898, 1899) were based on tooth morphology, and the number of teeth, dorsal spines and gill rakers. The genera were defined as follows:

Perissodus Boulenger 1898 (p. 21), type (and only) species *microlepis,* by original designation, has broad-based, enlarged, truncated teeth with the formula $\frac{18-26}{16-18}$, 18–21 gill rakers and 17–19 dorsal fin spines.

Plecodus Boulenger 1898 (p. 22), type species *paradoxus* by original designation, has large laminar and inwardly curled teeth with the formula $\frac{18-20}{12-15}$, 20–23 gill rakers and 18–20 dorsal fin spines. This genus has four species.

Xenochromis Boulenger 1899, type (and only) species *hecqui* by original designation, has compressed recurved teeth with the formula $\frac{22-45}{19-40}$, 47–57 gill rakers and 16–17 dorsal spines.

With the discovery of *Plecodus multidentatus* by Poll (1952) the morphological and meristic gap between *Plecodus* and *Xenochromis* was bridged because *multidentatus* possesses relatively small recurved teeth with slender cylindrical bases (Plate 2, Fig. 29), 23–26 gill rakers, 16–17 dorsal spines and the dental formula $\frac{33-40}{30-35}$. The jaw dentition of the newly discovered spe-
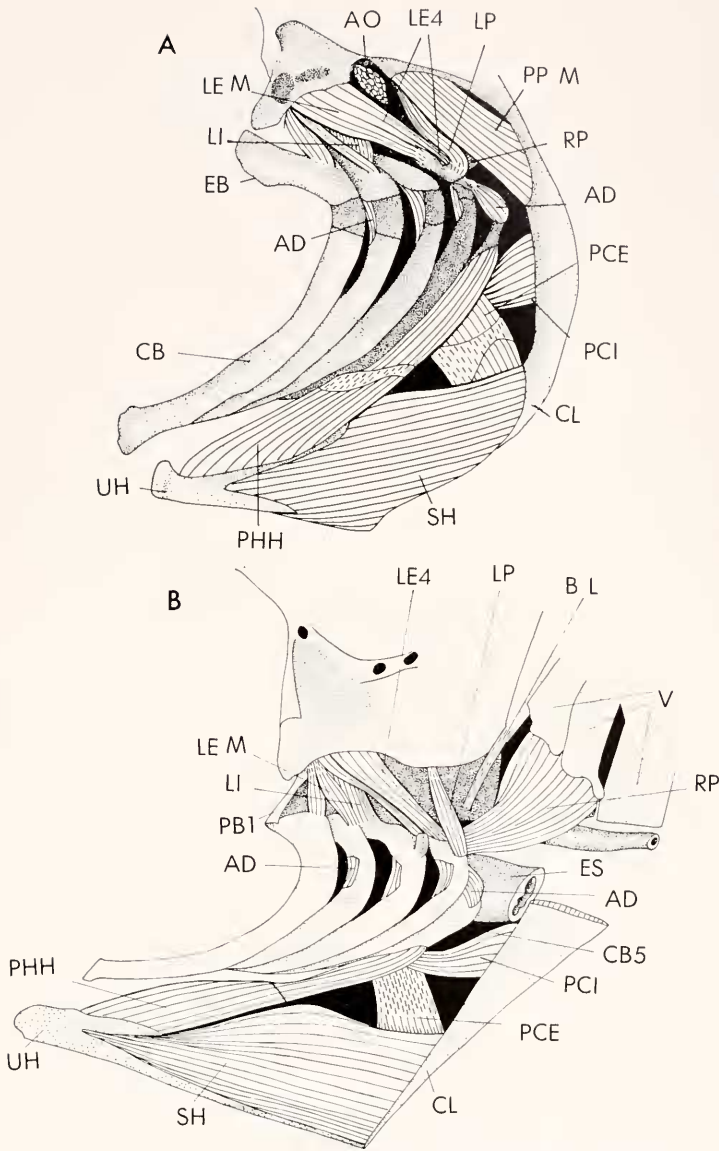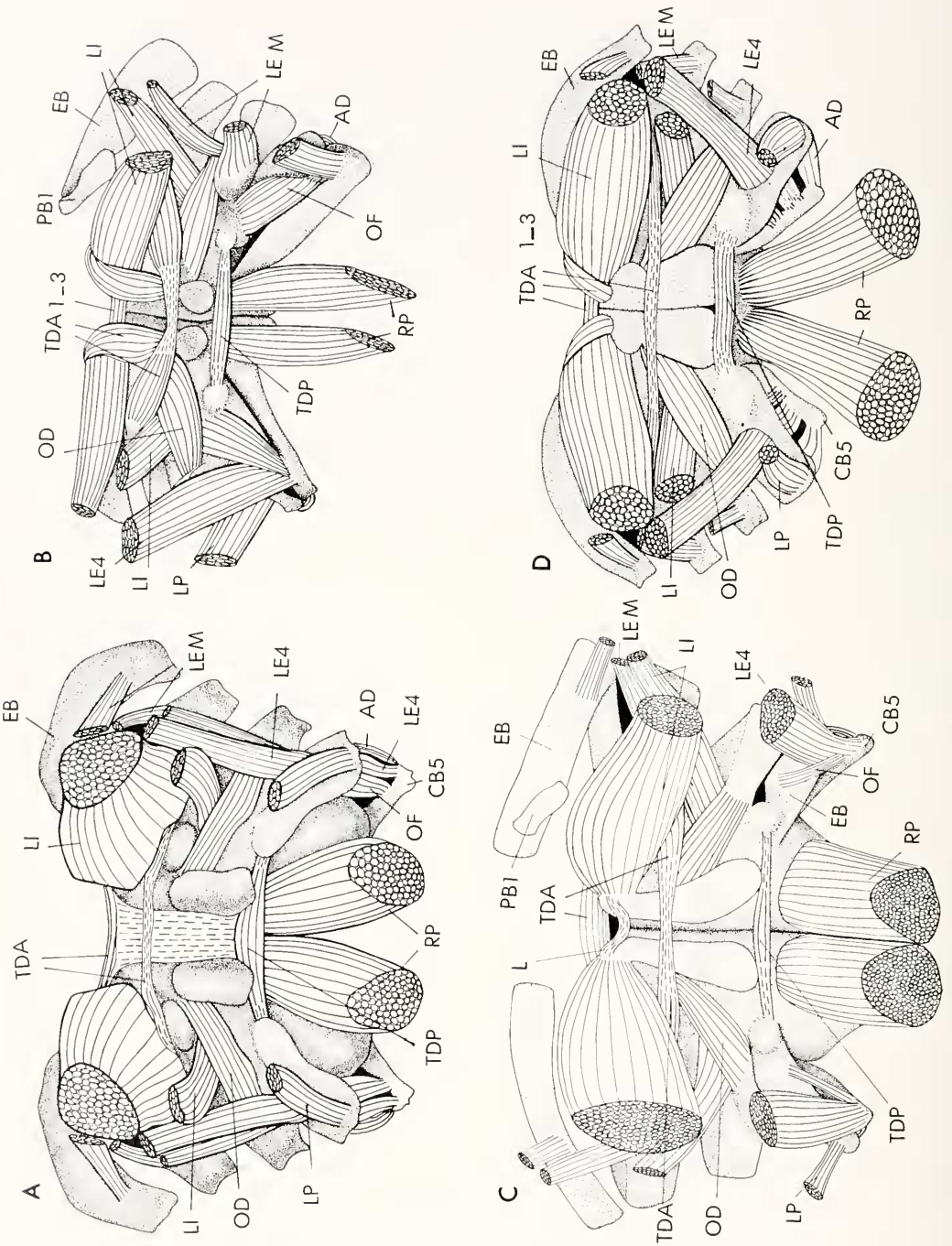
Figure 12. Lateral view of branchial apparatus and muscles after removal of operculum, suspensory apparatus, gills, gill rakers and mucous membrane. A, *eccentricus*; B, *microlepis*.

cies, *eccentricus*, bridges the gap between *Perissodus* and *Plecodus* especially since in a juvenile *eccentricus* the anterior mandibular teeth are broad-based with obtuse tips, whereas the lateral premaxillary teeth are strongly recurved (Plate 2; Figs. 25, 26, 28).

We have shown that the anatomy of the lepidophagous cichlids of Lake Tanganyika presents an unusual picture of a virtually complete morphological intergradation between the generalized (i.e., *hecqui*) and the specialized (i.e., *eccentricus*).

Now the question is whether all the con-

stituent species of this gradal complex (i.e., *hecqui, multidentatus, paradoxus, straeleni, elaviae, microlepis* and *eccentricus*) represent a truly monophyletic lineage or whether we are dealing with a web of parallelisms.

Our study of all known species comprising the lepidophagous cichlids of Lake Tanganyika has resulted in the discovery of the following unique combination of salient specializations shared by all members of the group: (1) The variously expanded jaw teeth arranged in a single row are either remarkably recurved, broadened, coiled or obtusely pointed in a truly unique fashion which doubtless facilitates the removal of scales from other fishes (Plates 1, 2; Figs. 23–31). Similarly-specialized tooth shapes have not been encountered in any other known cichlid; (2) The elongate maxilla possesses a posterior maxillary process, not shared with any other known cichlid of Lake Tanganyika (Figs. 5, 7:PP); (3) The parasphenoid exhibits an abrupt dorsal curvature at the level of the posterior orbit giving the neurocranium of this group a characteristic lateral profile (Figs. 2, 3:PS); (4) In the dorsal branchial musculature, the anterior levator internus muscle is dominant both structurally and functionally, a feature not shared by other cichlids of Lake Tanganyika (Fig. 13:LI); (5) An exceptionally thick ligament within the lower lip runs between the anterior tip of the dentary and the distal ends of the maxilla and premaxilla (Figs. 8, 9:MMM); (6) In the mandible the dentary is greatly enlarged, excluding the articular from the dorsal margin (Figs. 5, 6:D, this specialization is shared with algae-scraping cichlids of Lake Tanganyika ([Liem and Osse, 1975])); (7) The palatine has evolved additional processes to strengthen the palato-neurocranial connection. Similar conditions are found in algae-scraping cichlids, e.g.,

Eretmodus, Spathodus and *Tanganicodus;* (8) The intramandibularis (A_w) muscle is divided into two separate units. The ventral, and largest, of these originates from the quadrate and inserts on the ventro-medial aspect of the mandible. (Fig. 10B: IAM_1, IAM_2).

It is clear that this combination of eight specialized characters link all lepidophagous species of Lake Tanganyika into a monophyletic lineage. Because of this basic homogeneity in specialized morphology we exclude the possibility that several unrelated species are ancestors. Within this assemblage we can recognize two primitive and five derived species (see next section). On the evidence presented above, we include all the species of this monophyletic lineage in one genus. Since *Perissodus* Boulenger 1898 (p. 21) with the type species *microlepis*, has priority over *Plecodus* Boulenger 1898 (p. 22) and *Xenochromis* Boulenger 1899, the monophyletic lepidophagous lineage composed of *hecqui, multidentatus, paradoxus, elaviae, straeleni, microlepis* and *eccentricus* is classified within the genus *Perissodus*, which is defined by the above mentioned combination of specialized characters.

Interrelationships of *Perissodus* species

As the base line of this study we have identified as generalized those characters shared by *Haplochromis burtoni*, an insectivorous species with a riverine distribution but also occurring in Lake Tanganyika. Many of the myological features in *H. burtoni* resemble those of *Tilapia* as described by Goedel (1974a, b). Having established the morphological nature of a generalized species in Lake Tanganyika, we hope to determine the evolutionary directions of the various species of *Perissodus*.

←

Figure 13.   Dorsal view of dissected and isolated branchial apparatus and muscles. A, *eccentricus*; B, *hecqui*; C, *microlepis*; D, *multidentatus*.
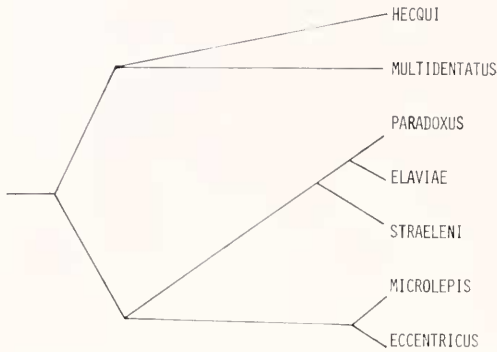
Figure 14. Proposed phyletic relationships within the genus *Perissodus*.

The greatest number of primitive characters has been found in *P. hecqui* and *P. multidentatus*. Both species retain (a) the generalized pattern of the three heads of the transversus dorsalis anterior muscle, (b) the well-developed obliquus posterior (Figs. 13B, D:TDA, OF), (c) a higher number of jaw teeth than other related species, (d) the elongate mandible, and (e) the rounded shape of the articular apophyses on the dorsal surfaces of the third pharyngobranchials (Fig. 13B, D). *P. hecqui* appears to be the most primitive representative of this lineage since it is the only species with a relatively unspecialized palatine, an unmodified adductor arcus palatini, and a preopercular with a shallow and relatively restricted adductor fossa. Although *P. hecqui* and *P. multidentatus* differ from each other in respect to dentition, number of gill rakers in the lower part of the first arch, and the distal configuration of the mandible, the two taxa can be regarded as sister species since they share the character of an increased number of gill rakers in the lower part of the first gill arch (Fig. 14).

In all other, more specialized species, the second head of the transversus dorsalis anterior is lost, the obliquus posterior becomes atrophied, and the mandible is shortened and deepened (Figs. 13, 5, 6). The articular apophyses on the dorsal surface of the third pharyngobranchial be-

comes elongate (Fig. 13A, C), the anterior levator internus is hypertrophied (Fig. 13:LI), and the greatly enlarged jaw teeth are either curled inwardly or become truncated or obtusely pointed (Plates 1, 2: Figs. 23–31).

We can recognize a clear dichotomy in the five specialized species. In one lineage comprised of the sister species *P. microlepis* and *P. eccentricus* (Fig. 14) tooth specialization involves a broadening of the tooth base while distally the tooth form becomes truncated or obtusely pointed. Both species usually have at least some premaxillary teeth recurved as in other *Perissodus* but never laminar as in the next species group. This second lineage, represented by *P. elaviae, P. paradoxus*, and *P. straeleni* (Fig. 14), exhibits such salient specializations as strongly curled laminar teeth and the loss of the third head of the transversus dorsalis anterior muscle. *P. straeleni* deviates from the sister species pair, *P. paradoxus-elaviae* in respect to the high supraoccipital crest extending anteriorly to the posterior rim of the rostral fossa.

Functional Analysis of Lepidophagous Mechanism

Stomach contents have established that all species of *Perissodus* except *hecqui* feed on fish scales (Marlier and Leleup, 1954; Poll, 1956). Our observations indicate that *P. hecqui* feeds predominantly on scales, although some individuals do eat copepods and insect larvae. The scales are definitely from percoid fishes and some have been identified as cichlid caudal fin scales. Some long, deep, ctenoid scales are almost certainly body scales of cichlids. We have not encountered clupeid or centropomid scales in the stomachs of *P. hecqui*. One species, *P. straeleni*, has been studied in an aquarium where it fed exclusively on scales (Fryer and Iles, 1972, p. 89). These fish remove scales by opening the jaws as widely as possible and pressing the mouth against the prey. Subsequent strong adduction of the jaws leaves a denuded spot

on the prey's body. From these observations we assume that *Perissodus* removes scales by biting rather than by rasping small scales from the two sides of the caudal fin, a method used by *Corematodus* in Lake Malawi and *Haplochromis welcommei* in Lake Victoria.

The functional prerequisites for collecting scales by a biting mechanism are a powerful and stable adductor system and a capability to open the mouth widely and variedly so that the upper and lower jaws can be pressed intimately against the surface of the body of the prey.

Extreme abduction of the mandible is made possible by relatively deep articulatory surfaces of the anguloarticular, permitting the mandible to rotate around the quadratomandibular joint in a wider angle (Greenwood, 1967). In the upper jaw, the ascending processes of the premaxillae are greatly shortened (Figs. 7, 8, 9:APPM). Short ascending processes of the premaxillae free the premaxilla from constraints on rotation around a transverse axis. The distal tip of the alveolar process of the maxilla can then be rotated anteroventrally over a much longer distance to occupy a nearly vertical position, matching a similar position of the fully abducted mandible. Apart from the deeper articulatory configuration of the quadratomandibular joint and the shortened ascending processes of the premaxillae, no other specializations can be correlated with the ability to open the jaws widely. The jaw opening mechanisms depend on the action of three couplings as discussed by Liem (1970), and Liem and Osse (1975).

The abducted jaws are stabilized by the hypertrophied collaginous tract within the lower lip (Figs. 8, 9:MMM), and strongly developed medial and anterior maxillomandibular ligaments. The strongly abducted mandible creates some mechanical problems for the adductor system. During the wide-open phase of the mouth the insertion site of pars A_2 of the adductor mandibulae muscle is close to the quadrato-

mandibular joint, resulting in a drastically diminished moment arm. Contraction of the adductor mandibulae pars A_2 muscle will therefore be very ineffective in closing the widely opened jaws. The hypertrophied second head of the intramandibularis muscle (Fig 10A, B), on the other hand, can change the direction of the working line of the pars A_2 of the adductor mandibulae muscle. The adaptive significance of the enlarged and separate new division of the intramandibularis muscle lies in its ability to create a favorable working line for the adductor mandibulae muscle when it pulls up the fully abducted mandible.

In most *Perissodus* it can be inferred from stomach contents that scales have been manipulated and arranged on top of each other to form discrete packets. The pharyngeal jaw apparatus (composed of the firmly united and toothed fifth ceratobranchials, the upper toothplates of the second, third and fourth branchial arches, and the muscles associated with all of these [see Liem, 1973]) may manipulate the scales to form manageable packets prior to deglutition. Special adaptations of the pharyngeal jaw apparatus have evolved to enhance this process. Within the lepidophagous lineage we can detect a distinct trend towards: (a) elongate articular surfaces of the basipharyngeal joint (Liem, 1973) which enhance longitudinal movements (Fig. 13:A, C); (b) the loss of one or two heads of the transversus dorsalis, drastic reduction of the remaining head(s) and the transversus dorsalis posterior muscle (Fig. 13); (c) hypertrophied anterior levator internus, retractor dorsalis, rectus communis and pharyngocleithralis internus muscles (Figs. 12, 13).

Greater control and mobility of the upper pharyngeal jaw is the most important specialization correlated with superior scale manipulating capabilities. Based on electromyographical evidence we can conclude that the retractor dorsalis (Liem, 1973) and the anterior levator internus (Liem, in preparation) are antagonistic muscles,
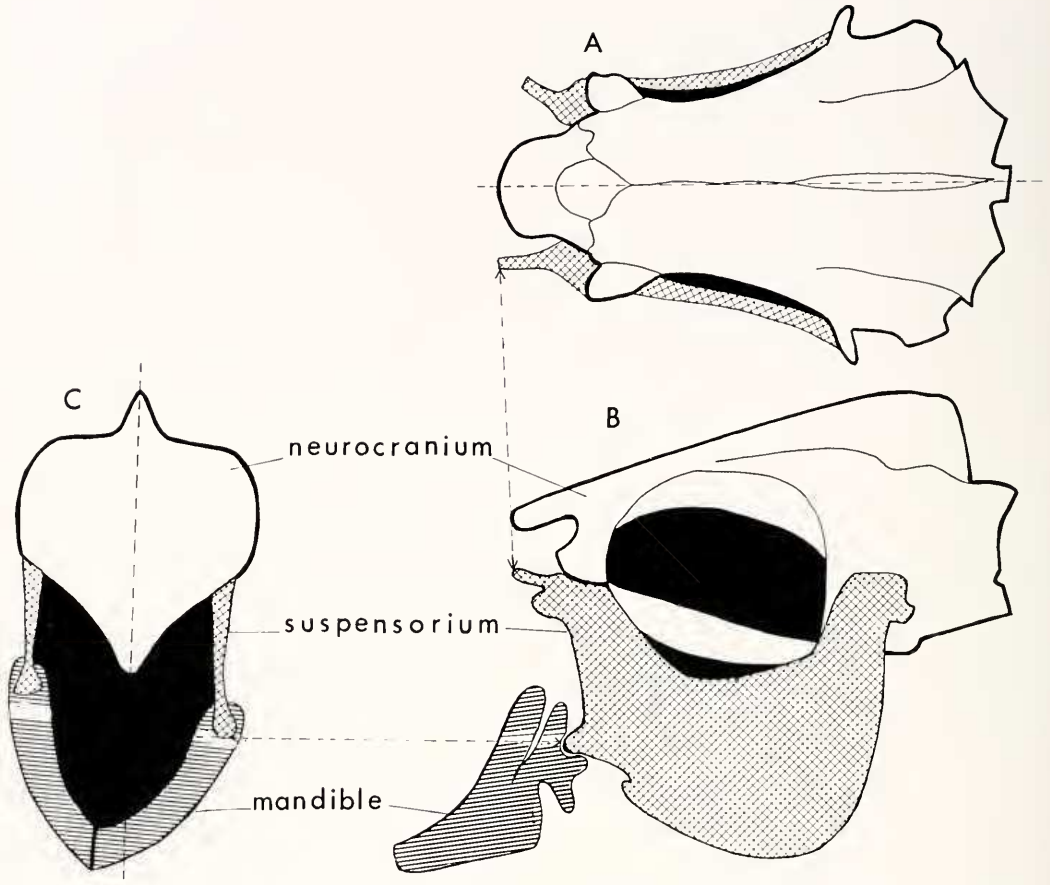
Figure 15. Diagrammatic representation of asymmetry in *eccentricus*. A, dorsal view of neurocranium, suspensory apparatus and mandible; B, lateral view of neurocranium, suspensory apparatus and mandible; C, frontal view of neurocranium and suspensory apparatus.

which, in conjunction with the elongate articular surfaces of the pharyngeal jaws, can produce controlled and more extensive protraction, retraction and adduction of the upper pharyngeal jaws. Because the upper pharyngeal jaws of either side can be controlled independently (Liem, in preparation), the additional specializations give the lepidophagous pharyngeal jaw apparatus the necessary controlled mobility to manipulate scales into packets. Morphological reduction of all constrictors seem to indicate that movements produced by long-fibered muscles are selected for, while movements produced by shorter fibered ones

play a much diminished role. The lower pharyngeal jaw apparatus does not deviate much from the pattern characterizing all cichlids. However, more extensive movements, in coordination with those of the upper pharyngeal jaws, are realized by the hypertrophied and elongated rectus communis and pharyngocleithralis internus muscles (Fig. 12). Coordinated actions of the fourth levator externus, pharyngocleithralis internus and the rectus communis with its posterior attachment on the fifth ceratobranchial (Fig. 12:LE_4, PCI, PHH) enable the upper and lower pharyngeal jaws to remain in close or near

apposition for long periods during the manipulatory cycle. Meanwhile, the anterior levator internus and retractor dorsalis cause the controlled longitudinal and rocking movements around the elongate basipharyngeal joint. Within the lepidophagous lineage, *P. hecqui* and *P. multidentatus* have a rounded and small articular apophysis of the basipharyngeal joint (Fig. 13B, D), suggesting that they may have only limited abilities to arrange scales in packets. Stomach contents of *P. hecqui* do not reveal scales in packets, but more studies are required to verify this preliminary observation.

Functional Significance and Evolutionary Origin of Jaw Asymmetry

Asymmetry of the jaw apparatus of *P. eccentricus* is unique among the large order Perciformes. When the mouth is opened, the upper and lower jaws deviate either to the left or to the right side respectively in sinistral and dextral individuals (represented in equal numbers in our population sample [Plate 1: Figs. 17, 18, 19, 20, 22]). As asymmetry of jaw opening and protrusion is accompanied by asymmetrically arranged teeth (Plate 1: Figs. 20, 22), a given individual can bite scales from just one side of its prey depending on direction of approach (i.e., front or back). Asymmetrical jaws may provide *P. eccentricus* with a mechanism by which it can approach its prey much more stealthily than its symmetrical counterparts; it should be able to strike very effectively while its body is parallel to that of its prey. If prey can only be approached from behind, a sinistral *P. eccentricus* could only strike them on the right side. It would therefore be understandable that sinistral and dextral individuals occur in the same frequencies as such a distribution makes the best use of food resources.

It was noted that a few preserved *P. elaviae* also had jaws projecting slightly to one side when open but none had noticeably asymmetrical teeth. *P. elaviae* appears
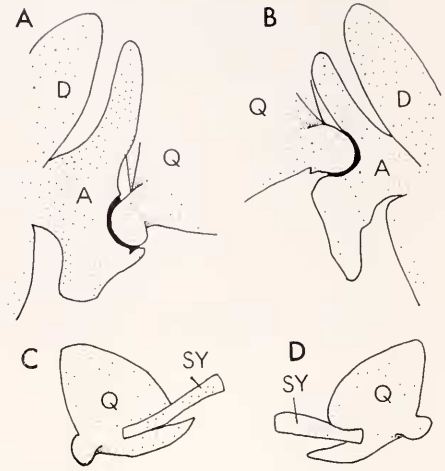

Figure 16. Lateral view of quadratomandibular region in *eccentricus.* (A, left; B, right) and symplectic-quadrate complex (C, left; D, right). (Dextral specimen.)

to be a deep-water counterpart of *P. paradoxus* in the same way that *P. eccentricus* is distributed deeper than its sister species, *P. microlepis*, although the depth distributions of *P. elaviae* and *P. paradoxus* overlap somewhat.

Functionally, the asymmetrical opening of the jaws uses the following mechanism. In a dextral individual, the right mandible can be dropped farther ventrally than the left one because the deeper articulatory socket of the right articular (Fig. 16) gives the right mandible a wider abduction angle (Greenwood, 1967, p. 53). In dextral individuals the distance between the quadratomandibular joint and the place where the interoperculum attaches to the suboperculum is larger on the right side than on the left. Consequently, the "kinematic efficiency" is higher on the right side. (Kinematic efficiency is defined by Anker [1974] as the ratio of the distance between the operculomandibular joint and the attachment of interopercular to operculum on one hand, and quadratomandibular joint and the attachment of interoperculum to operculum on the other hand.) In dextral individuals, a higher kinematic efficiency on the right side means that a *smaller*

PLATE 1

Fig. 17. Lateral view of dextral *P. eccentricus*.

Fig. 18. Lateral X-ray photograph of same specimen as Figure 17.

Fig. 19. Frontal view of same specimen as Figure 17.

Fig. 20. Ventral view of upper jaw of *P. eccentricus*.

Fig. 21. Scanning electron micrograph of lateral aspect of lateral premaxillary teeth of *P. eccentricus*.

Fig. 22. Dorsal view of lower jaw of *P. eccentricus*.

Fig. 23. Scanning electron micrograph of anterodorsal aspect of anterior mandibular teeth of *P. paradoxus*.

Fig. 24. Scanning electron micrograph of dorsal aspect of mandibular teeth of *P. hecqui*.
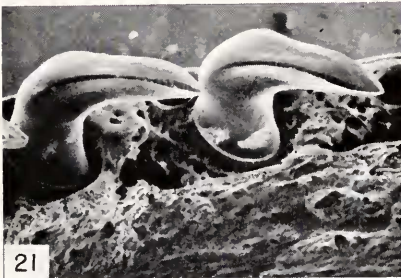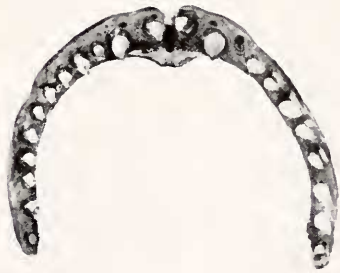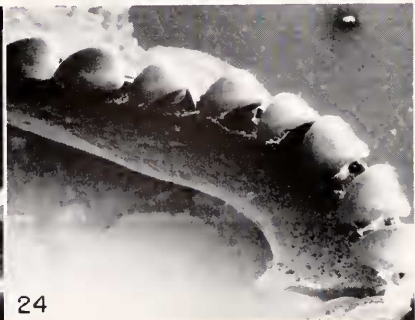
PLATE 2

Fig. 25.   Scanning electron micrograph of ventrolateral aspect of anterior premaxillary teeth of *P. eccentricus.*

Fig. 26.   Scanning electron micrograph of lateral aspect of second anterior premaxillary tooth of *P. eccentricus.*

Fig. 27.   Scanning electron micrograph of lateral aspect of anterior mandibular teeth of *P. hecqui.*

Fig. 28.   Scanning electron micrograph of lateral aspect of lateral premaxillary tooth of *P. eccentricus.*

Fig. 29.   Scanning electron micrograph of anterodorsal aspect of mandibular teeth of *P. multidentatus.*

Fig. 30.   Scanning electron micrograph of dorsolateral aspect of premaxillary teeth of *P. microlepis.*

Fig. 31.   Scanning electron micrograph of posterior aspect of anterior mandibular teeth of *P. hecqui.*
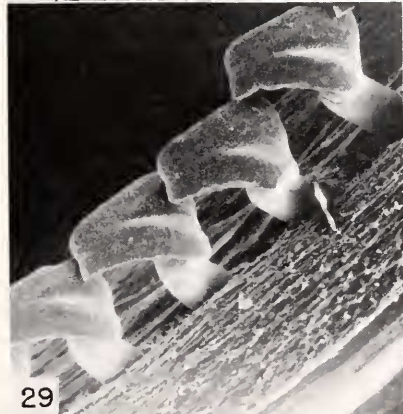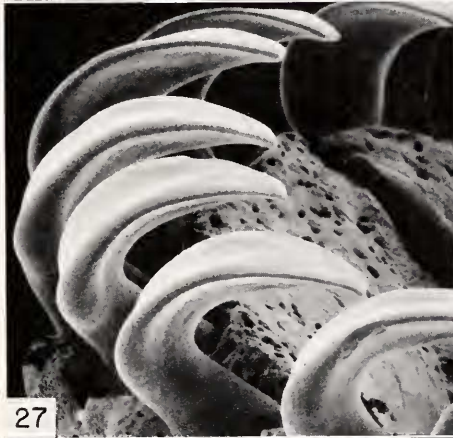
rotation angle for the right interopercular-subopercular and opercular series can achieve a *larger* rotation angle for the right half of the mandible. The superimposition of a deeper quadratomandibular joint upon the higher kinematic efficiency on a given side will result in a pronounced asymmetrical movement of the mandible. Since the upper jaw is morphologically and functionally coupled to the mandible (Liem, 1970), the asymmetrical movement of the latter will be automatically translated to the former. A special adaptive feature allowing for a highly efficient asymmetrical movement of the upper jaw is the asymmetrical suspension of the maxillae from the maxillary processes of the palatines (Fig. 15A, B). In a dextral individual, the maxillary process of the right palatine is turned more laterally than the left (Fig. 15A), thus reenforcing the asymmetrical forces transmitted from the mandible. The resulting mechanism assures a perfectly asymmetrical coordination of upper and lower jaws.

The morphological basis of this complex asymmetrical jaw apparatus is surprisingly simple. A configural change in the articulatory surface of the jaw-joint on one side has far reaching functional consequences leading to pronounced asymmetrical patterns in jaw movements. This functional asymmetry has been re-enforced by bilateral differences in the kinematic efficiency of the levator operculi-opercular apparatus-mandible coupling which opens the jaws. These efficiency differences result from a topographical shift of the quadratomandibular joint on one side (Fig. 15C). Asymmetrical differences in the relative position of the quadratomandibular joints are correlated with just two structural elements within the suspensory apparatus, i.e., in dextral individuals the left symplectic is longer and more oblique compared with the right one (Fig. 16). From the evidence presented by *P. eccentricus*, we may conclude that the asymmetrical position of the quadratomandibular joint is determined by growth centers associated with the symplectic-

quadrate complex. Such a simple ontogenetic cause supports the hypothesis that the underlying morphological principle in the evolution of the trophically complex and morphologically varied lacustrine cichlids is differential growth in various skull-elements (Greenwood, 1973, 1974; Liem, 1973; Liem and Osse, 1975). Since such salient differences can evolve by bilateral asymmetry in one individual, we may conclude that the discovery of this new species supplies further indirect evidence that simple genetic alterations can slightly affect the scheduling or velocity of ontogenetic events, which in turn are capable of producing adult phenotypic changes of rather profound dimensions.

SUMMARY

Scale-eating in lacustrine cichlid fishes is one of the most extraordinary trophic specializations evolved during the explosive phase of cichlid adaptive radiation, which resulted in optimal partitioning of all food resources. Within this distinctive scale-eating lineage, characterized by unique adaptations, we have recorded a sustained and prevailing evolutionary trend towards occupation of progressively narrower adaptive zones. A new, asymmetrical form seems to represent the summit of the scale-eating trend. Pronounced asymmetry of the jaw mechanism may have been selected for as a mechanism enabling the scale-eater to approach its prey in a strategically favorable fashion. The morphogenetic mechanisms underlying this asymmetry are bilateral differences in differential growth rates of two bones in the jaw suspension and the remodeling of articular surfaces of the lower jaw joints. It is postulated that such mechanisms are controlled by relatively simple genetic factors governing the velocity or timing of ontogenetic events. Asymmetry has furnished the flatfishes (Pleuronectiformes) with a most effective mechanism to exploit the benthic habitats in an extremely efficient way. The capacity of cichlids to evolve asymmetry of the jaw

mechanism rapidly by simple morphogenetic alterations represents another example that fewer adaptive compromises are necessary if more parameters controlling form can vary independently. However, the potential to evolve asymmetry of jaws to optimize trophic functions rapidly has not been realized in other cichlids, indicating that asymmetrical jaws possess only a limited selective value in lacustrine habitats. It is possible that the process of specialization has reached its summit in this new species (which may be at the end of an evolutionary blind alley), although we must be aware of the subjectivity of our judgment of specialization, and the limitations of our imagination.

KEY TO SPECIES OF *PERISSODUS* BOULENGER 1898

1. S.L./depth 3.0–4.35; less than 9 scales between lateral line and dorsal fin origin .. 2
–   S.L./depth 2.5–2.95; 10–11 scales between lateral line and dorsal fin origin; max. size 160 mm .... *P. straeleni* (Poll) 1948.
2. Teeth small, contiguous, all about equal size, 18–40 on mandible 3
–   Teeth large, spaced, of unequal sizes, 12–23 on mandible 4
3. Mandible broadly rounded; 47–57 gillrakers on lower part of first arch; lateral line 57–65; max. size 280 mm ....
 .... *P. hecqui* (Boulenger) 1899.
–   Mandible narrow, pointed; 23–26 gillrakers on lower part of first arch; lateral line 69–73; max. size 139 mm ....
 .... *P. multidentatus* (Poll) 1952.
4. Anterior mandibular teeth laminar strongly curled inward 5
–   Anterior mandibular teeth truncated or obtusely pointed, not laminar or curled inward 6
5. Upper and lower jaw teeth 18–20/12–15; A.III, 12–13; lateral line 68–78; S.L./depth 3.75–4.15; max size 290 mm ....
 .... *P. paradoxus* (Boulenger) 1898.
–   Upper and lower jaw teeth 22–37/18–23; A.III, 10–11; lateral line 64–67; S.L./depth 3.0–3.8; max. size 320 mm ....
 .... *P. elaviae* (Poll) 1949.
6. Lateral mandibular teeth bilaterally symmetrical; 17–18 dorsal spines; upper and lower lateral lines 45–51/22–32; max. size 111 mm .... *P. microlepis* Boulenger 1898.
–   Lateral mandibular teeth asymmetrical; 14–15 dorsal spines; upper and lower

lateral lines 51–60/32–45; max. size 128 mm .... *P. eccentricus* n. sp.

ACKNOWLEDGMENTS

LITERATURE CITED

ANKER, G. CH. 1974. Morphology and kinetics of the head of the stickleback, *Gasterosteus aculeatus*. Trans. zool. Soc. Lond., **32:** 311–416.

BOULENGER, G. A. 1898. Report on the collection of fishes made by Mr. J. E. S. Moore in Lake Tanganyika during his expedition, 1895–1896. Trans. zool. Soc. Lond., **15:** 1–30.

BOULENGER, G. A. 1899. Matériaux pour la faune du Congo: Poissons nouveaux. Ann. Mus. Congo. Zool. Sér. 1, fasc. **5**: 97–128.

FRYER, G., AND T. D. ILES. 1972. The cichlid fishes of the great lakes of Africa. Oliver and Boyd, Edinburgh, 641 pp.

GOEDEL, W. 1974a. Beiträge zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei). Teil 1. Zool. Jb. Anat., **92**: 220–274.

GOEDEL, W. 1974b. Beiträge zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei). Teil 2. Zool. Jb. Anat., **92**: 321–383.

GREENWOOD, P. H. 1967. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part VI. Bull. Br. Mus. nat. Hist. (Zool.), **15**: 29–119.

GREENWOOD, P. H. 1973. Morphology, endemism and speciation in African cichlid fishes. Verh. Deutsch. Zool. Gesellsch, **1973**: 115–124.

GREENWOOD, P. H. 1974. The cichlid fishes of Lake Victoria, East Africa· The biology and evolution of a species flock. Bull. Br. Mus. nat. Hist. (Zool.) Suppl. **6**, 134 pp.

LIEM, K. F. 1970. Comparative functional anatomy of the Nandidae (Pisces: Teleostei). Fieldiana: Zool., **56**: 1–166.

LIEM, K. F. 1973. Evolutionary strategies and morphological innovations: Cichlid pharyngeal jaws. Syst. Zool., **22**: 425–441.

LIEM, K. F., AND J. W. M. OSSE. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. Am. Zool., **15**: 427–454.

MARLIER, G., AND N. LELEUP. 1954. A curious ecological "niche" among the fishes of Lake Tanganyika. Nature, Lond., **174**: 935–936.

POLL, M. 1946. Révision de la faune ichthyologique du lac Tanganika. Annls. Mus. r. Congo Belge Sér. 4, **3**: 141–364.

POLL, M. 1950. Histoire du peuplement et origine des espèces de la faune ichthyologique du Lac Tanganika. Annls. Soc. r. zool. Belg., **81**: 111–140.

POLL, M. 1952. Quatrième série de Cichlidae nouveaux recueillis par la mission hydrobiologique belge au Lac Tanganika (1946–47). Bull. Inst. r. Sci. nat. Belg., **28**: 1–20.

POLL, M. 1956. Poissons Cichlidae. Résultats scientifiques Explorations hydrobiologique du Lac Tanganika (1946–1947), **3**, Fasc. 5b: 1–619.

REGAN, C. T. 1920. The classification of the fishes of the family Cichlidae. I. The Tanganikan genera. Ann. Mag. nat. Hist., **5**: 33–53.

THYS VAN DEN AUDENAERDE, D. F. E. 1964. Révision systématique des espèces Congolaises du genre *Tilapia* (Pisces, Cichlidae). Annls. Mus. r. Afr. cent. Se. Zool., **124**: 1–155.

VANDEWALLE, P. 1972. Ostéologie et myologie de la tête de *Tilapia guineensis* Bleeker (Pisces, Cichlidae). Annls. Mus. r. Afr. cent. Se. Zool., **196**: 1–50.

WICKLER, W. 1963. Zur Klassifikation der Cichlidae, am Beispiel der Gattungen *Tropheus*, *Petrochromis*, *Haplochromis* und *Hemihaplochromis* n. gen. (Pisces, Perciformes). Senckenberg. biol., **44**: 83–96.

WINTERBOTTOM, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Philadelphia, **125**: 225–317.